Scripta Geobot. 21 (1993): 29–38

Cyclic succession in heathland under enhanced nitrogen deposition: a case study from the Netherlands

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Summary

Atmospheric nitrogen deposition (on average 35 kg ha^{-1} yr^{-1}) has been seen as the most important factor causing the vigorous growth of grasses in Dutch heathlands, which is changing at least the heather communities into grassland. Recently, however, local observations have revealed the beginning of a trend in the opposite direction: the progressive dying-off of *Deschampsia flexuosa* and spontaneous regeneration of *Calluna vulgaris*. This paper presents an analysis of the spontaneous development of a grassy heathland community based on two inventories (using the point-quadrat method) carried out in 1982 and 1991. Five subsystems have been distinguished, representing particular successional stages of the community development and differing in species composition, growth and vitality of *Calluna vulgaris* and *Deschampsia flexuosa*, nutrient status and cycling: (1) a subsystem dominated by *Calluna* in decline, (2) a subsystem dominated by mature *Deschampsia*, (3) a subsystem dominated by *Deschampsia* in decline, (4) a subsystem without any vegetation, and (5) a subsystem dominated by young *Calluna*. The continuous shift in cover, vitality and growth of *Calluna* and *Deschampsia* indicates a cyclic process in the development of the ecosystem investigated, despite the fact that the nitrogen climate in the area has not changed. To reveal causes and mechanisms of species alternation in heathland ecosystems and the exact role of enhanced N deposition in this process, the authors emphasize the necessity of research in spontaneous dynamics of heathlands. They hypothesize that the changing nutrient status during the succession, combined with the physical age of particular species, could be the driving force behind the species alternation during the spontaneous succession on dry heathland ecosystems.

Atmospheric N deposition, *Calluna vulgaris*, *Deschampsia flexuosa*, grassland, heathland, species alternation, spontaneous succession.

Introduction

In the last 20 years Dutch heathlands have been going through a dramatic change characterized by an excessive growth of grasses which are ousting heather. By 1991, some 30% of the 42000 ha of heathland had already changed into grassland; another third appeared set to become grassland within three to five years, and only the remaining third was still a vital heathland (Dobben 1991). On dry heathlands *Calluna vulgaris* has been mostly replaced by *Deschampsia flexuosa*, while on the moist ones, *Molinia caerulea* has become dominant over *Erica tetralix*.

Although a number of factors can stimulate this change, acid deposition, especially nitrogen emission, has been seen as the key factor behind this change (among others Berendse & Aerts 1984; Berendse et al. 1987; Aerts 1989). Apart from areas of excessive N emission, such as the Peel in North Brabant province, the average N deposition in the Netherlands varies around 35–40 kg N ha^{-1} y^{-1} (Dobben 1991). The 'atmospheric N fertilization' is thought to be responsible for disturbing the spontaneous development of heathland in which *Calluna* regeneration naturally follows after old heather shrubs had died off. This pattern of spontaneous dynamics has been described by Barclay-Estrup & Gimingham (1969), Miller & Miles (1970) and in detail by Gimingham (1972) in Scotland and is thought to be general model of the spontaneous dynamics of the atlantic *Calluna*-dominated heathlands. In view of this model, the rank growth of grasses has been seen as a disturbance in community development, which may only be caused by an external factor, in this case by excessive N deposition.

There is no doubt that the addition of N changes ecological relations among species in the community, stimulating the fast-growing species and retarding the growth of the slow-growing ones (Dobben 1991). However, the question arises whether this may be seen as a key factor in the process of species alternation. Replacing *Calluna* by *Deschampsia* in the course of spontaneous heathland development is not a new phenomenon solely related to the present-day 'acid deposition period'. Long before this period, the phenomenon was known to old Dutch shepherds (Harteveld, pers comm.). Stoutjesdijk (1959) described a cyclic replacing of *Calluna* by *Deschampsia* and vice versa in the Veluwe area. Gimingham (1972) reported that *Deschampsia* prevents the reappearance of *Calluna*. A shift from *Calluna* to *Deschampsia* after heather beetle (*Lochmaea suturalis*) attack or after frost damage on *Calluna* has been broadly studied and generally recognized (e.g. Smidt 1977; Berdowski & Zeilinga 1987). Based on N and P fertilizer experiments, Heil & Diemont (1983) documented unequivocally that raised nutrient levels change heathland into grassland – a conclusion which also supports the 'atmospheric N fertilization' hypothesis.

Contrary, in their experimental studies on competition among heathland species, Aerts et al. (1990) concluded that intact *Calluna* growth appears to be competitively superior to *Deschampsia* and even *Molinia* plants, even at higher levels of nitrogen availability. Their results reveal that the replacement of *Calluna* by grasses cannot be explained by nitrogen availability alone. They concluded that such a replacement can only take place when the increased N availability occurs simultaneously with openings in the *Calluna* canopy caused e.g. by severe frost, drought or by grazing of the heather beetle. According to Berendse (1990) high rate of N mineralization is the key factor in species replacement in heathlands.

Very recently detailed observations in the dry grassy heathlands in the Netherlands have revealed a new phenomenon in the grass growth: although the emission climate has not changed substantially, *Deschampsia* is locally losing its formerly vigorous growth. The grass cover deteriorates and even dies off, being followed by mosses, lichens and *Calluna* seedlings. This development brings a new view on the problem and generates questions about the internal dynamics of heathland ecosystems and about other driving forces steering the change.

Research site and methods

In 1982, an old unmanaged and abandoned heathland in Central Netherlands was chosen for the research (Landgoed Planken Wambuis, (52°04'N, 5°45'E). The site is located on a Pleistocene (Saalien) moraine ridge (Fig. 1). The brown podzolic soil is formed by coarse sand, slightly loamy, with an admixture of gravel. Earlier, the area was used as heathland. It has been abandoned since the fifties.

Eight permanent quadrats of 2 x 2 m were established in 1982 in different types of *Calluna* and *Deschampsia* vegetation, having different species composition and vitality. The point-quadrat (PQ) method (Goodall 1953; Mueller-Dombois & Ellenberg 1974) was used for an inventory of the spatial structure of the vegetation cover. 100 points were recorded in each PQ, each point record including plant species, their heights (in cm), vitality, and the thickness of the organic layer. The vitality of *Calluna* and *Deschampsia* was classified in six classes (see Tab. 1).

The first inventory was carried out in 1982, the second in 1991. Samples of the ectorganic layer were taken in 1982 to establish total organic matter, pH, N-total, C and C/N ratio. In 1991 a more detailed sampling was carried out, stratified into F, H and A layers. In total, 184 soil profiles were described and sampled to establish the content of the dry and the organic matter, pH, N, C/N, P, K, Na, Ca, Mg, Fe, Mn and Al. Standard methods of the chemical analysis were used during the laboratory work.

The results presented here are preliminary and so far only involve the organic profile analysis. In the follow-up the biomass will also be analysed.

Results and discussion

Vegetation composition and structure

Tab. 2 gives the results of inventories in 1982 and 1991. It shows considerable changes in species composition and cover. In 1982, dying and dead *Calluna* covered a considerable area of plots 1–5, being successively replaced by *Deschampsia*. This change was accompanied by a vigorous growth of mosses. In other plots, this change apparently happened earlier. Thereafter, *Deschampsia* dominated the plots and the cover of mosses and lichens was very poor. No open places in vegetation were found in 1982. Spontaneous regeneration of *Calluna* consisted of a few young plants. The inventory of 1991 revealed a

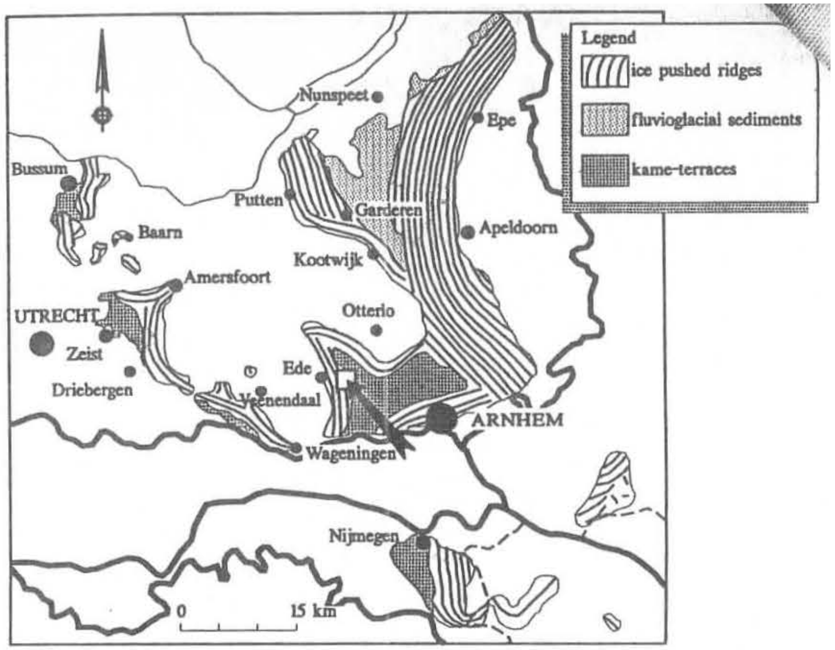

Fig. 1: Glacial geomorphology of Central Netherlands.

Tab. 1: Vitality classes of *Calluna vulgaris* and *Deschampsia flexuosa*

	Calluna vulgaris	*Deschampsia flexuosa*
5	very vital, fertile, closed canopy, vigorous growth	very vital, fertile, closed canopy, stalks ca. 60 cm tall
4	vital, fertile closed canopy	vital, fertile, closed canopy, stalks ca. 40–60 tall
3	first signs of decreasing vitality, low fertility, openings in the canopy	first signs of decreasing vitality, low fertility, openings in the canopy, stalks ca. 20–40 cm tall
2	low vitality, still alive, but many branches dead, shrubs wide open	low vitality, clumps still alive, but drying, scattered stalks ca. 20–30 cm tall, ears sterile
1	shrubs dying, branches lying on the grond, open patches	clumps dying, sterile, no stalks, open patches among the clumps
0	dead	dead

Tab. 2: Species and cover inventory 1982 and 1991 (in %).

1982

Plot nr	*Calluna* (dead)	*Deschampsia*	Other plants	Mosses & lichens	Litter & sand	*Calluna* (young plants & seedlings)	Remarks
1	89	24	13	79 1)	–	5	1) average cover of lichens 4
3	90	71	10	32	–	6	
5	76	87	–	45	–	–	
7	8	99	8	23	–	–	
9	11	100	–	15	–	–	
11	6	98	8	12	–	1	
13	–	97	8	23	–	–	
15	–	99	1	3	–	–	

1991

1	–	84	4	98 1)	–	71	1) average cover of lichens 11
3	1	90	19	78	–	77	
5	–	82	1	78	4	2	
7	–	94	16	53	1	2	
9	–	82	5	58	2	12	
11	–	88	–	51	4	17	
13	–	78	8	48	1	6	
15	–	72	4	44	15	7	

quite different situation. Dead *Calluna* had disappeared completely and had been overgrown by *Deschampsia*, mosses and lichens and, in plots 1 and 3, young shrubs of *Calluna*. In other plots, *Deschampsia* cover had diminished, leaving room for a considerable cover of mosses, lichens and some vascular plants. Open places in vegetation (covered with dead organic material, or bare sand) appeared here, giving room for seedlings of *Calluna* to establish.

These trends are still more obvious from Tab. 3 showing, in addition the cover, considerable changes in vitality and heights of the two most important species – *Calluna vulgaris* and *Deschampsia flexuosa* within the period of ten years. Changes in vitality are striking:

Calluna:	old degenerated and dead shrubs in 1982; many young plants of high vitality in 1991.
Deschampsia:	high vitality in 1982; degeneration in most plots in 1991.

The change in vitality of *Deschampsia* has been accompanied by a considerable decrease of plant height in most plots and loss of fertility. In 1991, the *Deschampsia* cover was mostly formed by sterile clumps without any stalks. Tab. 3 indicates the beginning of a regeneration of *Calluna* after a period of dominance of grass vegetation, despite the persisting nitrogen deposition in the area.

Change in the composition of the F and H horizons

The description of 184 soil profiles revealed a difference in the composition of the organic materials constituting the F and H horizons. These materials originated from the earlier vegetation; remnants of *Deschampsia* (sheaths) and *Calluna* (bark, thick branches) were found during the profile description. In 115 profiles (out of 184), the decomposing material could be identified in both F and H layers. 109 profiles contained remnants of *Deschampsia* and *Calluna*; 6 profiles contained materials of various origin and were omitted.

Tab. 3: Cover (%), vitality and height (cm) in *Calluna* and *Deschampsia*.

Calluna vulgaris-old

Plot nr.	1	3	5	7	9	11	13	15
Cover 1982 1991	89 –	90 1	76 –	8 –	11 –	6 –	– –	– –
Vitality 1982 1991	0 –	0 0	0 –	0 –	0 –	0 –	– –	– –

Deschampsia flexuosa

Plot nr.	1	3	5	7	9	11	13	15
Cover 1982 1991	24 84	71 90	87 82	99 94	100 82	98 88	97 78	99 72
Vitality 1982 1991	4.2 1.0	4.5 1.6	4.8 1.4	4.8 1.9	4.1 1.5	3.1 2.2	2.8 1.2	0.6 2.3
Height 1982 1991	53 13	41 21	7.8 16	64 18	45 13	22 22	21 10	7 19

Calluna vulgaris-young

Plot nr.	1	3	5	7	9	11	13	15
Cover 1982 1991	5 71	6 77	– 3	– 2	– 12	1 17	– 6	– 9
Vitality 1982 1991	4.2 5.0	3.3 5.0	– 5.0	– 5.0	– 5.0	4.0 5.0	– 5.0	– 5.0
Height 1982 1991	7 25	7 23	– 11	– 6	– 6	10 8	– 6	– 3

The result of these simple statistics presented in Tab. 4 clearly reveals a continuous alternation of organic materials constituting the F and H horizons in the course of development of heathland ecosystem investigated. Under the mature and decaying *Deschampsia*, F horizons were, of course, formed by remnants of this species. But remnants of *Calluna* were found in most of the H horizons. This is evidence that *Deschampsia* is growing in places formerly occupied by *Calluna*. A similar situation was observed in places where *Deschampsia* had recently died. The analysis of the last group shows that young *Calluna* plants have germinated and are growing on F horizons originating from *Deschampsia*: one-quarter of the profiles investigated in this group had H horizons in which remnants of former *Calluna* generation were identified. This situation gives an alternation sequence *Calluna* – *Deschampsia* – *Calluna*, testifying to a cyclic process.

Nitrogen environment

No direct measurements of N deposition in the area investigated are available. Because there are no concentrated sources of N emission in the surroundings, we assume that the average N deposition in the area does not diverge substantially from the average figures of 35–40 kg ha^{-1} y^{-1} recently given by Dobben (1991).

Tab. 4: Ectorganic profiles: number of profiles with identified remnants of *Calluna* and *Deschampsia*.

under mature and/or decaying *Deschampsia*				
Fd	Fd	Fcd	Fd	unidentified F, H or both
Hc	Hcd	Hc	Hd	
25	5	2	14	18
Total 64				

without any vegetation				
Fd	Fd	Fcd	Fd	unidentified or incomplete
Hc	Hcd	Hc	Hd	
18	4	6	7	26
Total 61				

under young *Calluna*			
Fd	Fd	Fcd	unidentified F, H or both
Hc	Hcd	Hd	
10	3	11	26
Total 50			

F = fermentation horizon H = humus horizon c = *Calluna* remnants d = *Deschampsia* remnants

Tab. 5: Total amount of nitrogen, ashfree (kg/ha).

Subsystem	horizon	N-total
Old *Calluna*	F H A	604 969 12017
Mature *Deschampsia*	F H A	445 1155 13192
Deschampsia in decline	F H A	574 561 11161
Without any vegetation	F H A	313 1297 111401
Young *Calluna*	F H A	731 1373 15466

Tab. 5 gives a survey of N-total stocks per ha in 1991. These stocks originated partly from former vegetation, for an other part from N deposition. The figures show differences especially in F and H horizons both in different types of vegetation (*Calluna-Deschampsia*) and in their sucessional stages (young – mature – old), testifying for a great spatial variability of N stocks in the ecosystem investigated (despite of an overall deposition).

Competition experiments of Berendse & Aerts (1984), Aerts et al. (1990) and Dobben (1991) revealed an interesting phenomenon: rather low gifts of N seemed to be critical for an open *Calluna* canopy to be ousted by grasses. But an intact *Calluna* growth was not outcompeted even at a high N availability of 200–250 kg N ha^{-1} y^{-1} (Aerts et al. 1990) and in Dobbens (1991) experiments, a gift of 150 kg N ha^{-1} y^{-1} was necessary to outcompete *Calluna* when its canopy was closed. Light interception by a closed canopy should prevent strong growth of grasses. In the field, open canopy situations are mostly related either to young *Calluna* or to old, decaying *Calluna*, whereas the closed canopy is typical of a vital mature heathland. It is unlikely that a N addition in form of emission would be able to totally disrupt the spontaneous development of a mature, vital heather population. But this can happen easily in an old, overmature *Calluna* population of great physical age. Hence, the large scale replacement of heather by grasses in the Netherlands could be a matter of coincidence of these two phenomena: heathlands turned old at the same place as the environment deteriorated by increased N inputs. It seems that historical evidence would support this assumption. Thus, to understand the problem properly a deep insight is necessary not only into the nitrogen environment but also into the population dynamics of the main species constituting the community and the dynamics of the ecosystem as a whole.

Subsystems and their nutrient status and dynamics

The 'N deposition hypothesis' relates only to the shift from *Calluna* to *Deschampsia*. Decay of *Deschampsia* and the subsequent spontaneous regeneration of *Calluna* does not fit into the picture. Moreover, it casts doubt on the whole hypothesis: if the decay of *Deschampsia* and subsequent regeneration of *Calluna* instead are possible under the persisting N deposition, then the N emission cannot be the primary factor in the process of the continuous vegetation change in heathland. The question that then arises is: what is the driving force behind this change? Contrary to the previous assumptions, we hypothesize that the driving force(s) must be looked for not outside the system, but within it, in its own dynamics.

It is clear that the entire ecosystem investigated is in transition, exposing patches of different species composition, age, structure and vitality. Within the plots investigated we distinguished five different subsystems/development stages and submitted them to a detailed investigation. Tab. 6 gives the characteristics of these five subsystems.

Tab: 6: Subsystems/development stages identified.

Subsystem dominated by old *Calluna*

Calluna in decline with very low vitality; dying and dead;
accompanied by mosses and lichens.

Subsystems dominated by mature *Deschampsia*

Deschampsia vital; with tall stalks and fertile ears.

Subsystem dominated by *Deschampsia* in decline

Deschampsia with very low vitality and dying;
clumps sterile.

Subsystem without any vegetation

Soil surface covered with decomposing *Deschampsia* biomass;
patches of bare sand.

Subsystem dominated by young *Calluna*

Many *Calluna* seedlings established in bare sand and on decaying biomass;
young *Calluna* shrubs in full growth and of high vitality.

Tab. 7: Chemical analysis of organic profile (per subsystem).

		Subsysteme/development stages				
		old *Calluna*	mature *Deschampsia*	*Deschampsia* in decline	without any vegetation	young *Calluna*
thickness organic profile (cm)	F	3.0	2.3	3.3	0.7	1.3
	H	1.4	1.4	1.3	1.6	1.5
pH	F	3.6	3.5	3.2	3.1	3.6
	H	2.8	3.0	2.7	2.9	3.0
dry matter (ton/ha)	F	9	6	7	6	18
	H	26	33	14	48	41
organic matter (kg/ha)	F	22	15	21	9	13
	H	27	26	16	31	33
C/N	F	21.1	22.6	20.9	18.6	21.0
	H	20.3	18.1	20.5	19.5	18.6
N-total (kg/ha)	F	604	445	574	376	731
	H	969	1155	561	1513	1373
P (kg/ha)	F	23	19	21	13	36
	H	39	56	24	64	63
K (kg/ha)	F	40	28	31	17	46
	H	39	45	21	58	61
Ca (kg/ha)	F	75	22	28	14	70
	H	60	59	33	92	69
Mg (kg/ha)	F	19	10	13	6	22
	H	23	27	13	32	30
Mn (kg/ha)	F	12	7	7	2	14
	H	4	10	3	10	11

(N-total, P, K, Ca, Mg and Mn ashfree)

Chemical analysis revealed considerable differences among particular subsystems (Tab. 7). In the F horizons of subsystems without any vegetation, the nutrient content is less than under a vegetation cover. The lower content is probably caused by leaching because of no uptake by plants and because this horizon is thinner as decomposition is rapid.

The nutrient content (especially N and P) is highest in subsystems dominated by young *Calluna*. The nutrient content is lowest in subsystems dominated by *Deschampsia* in decay. The old *Calluna* and mature Deschampsia subsystems are intermediate in terms of nutrient content.

Finally, the pH in the subsystems dominated by old *Calluna* is not lower than in the *Deschampsia* subsystems or in the subsystems without vegetation. This is probably because there are remnants of *Deschampsia* organic matter which is not as acid as organic matter originating from *Calluna*.

Conclusions

Two inventories of the grassy heathland ecosystem investigated revealed considerable shifts in the species composition and spatial structure in the period between 1982 and 1991. The change in growth and vitality of both species, *Calluna vulgaris* and *Deschampsia flexuosa*, after ten years' development is striking: the average height and vitality of the dominating *Deschampsia* declined considerably and the 1991 *Deschampsia* cover is predominantly formed by sterile, decaying and dead clumps. In contrast, *Calluna* that was predominantly decaying and dead in 1982 seemed to be reviving in 1991. The inventory showed a continuous spread of young *Calluna* plants of excellent vitality and vigorous growth in places where *Deschampsia* had recently died off and decayed.

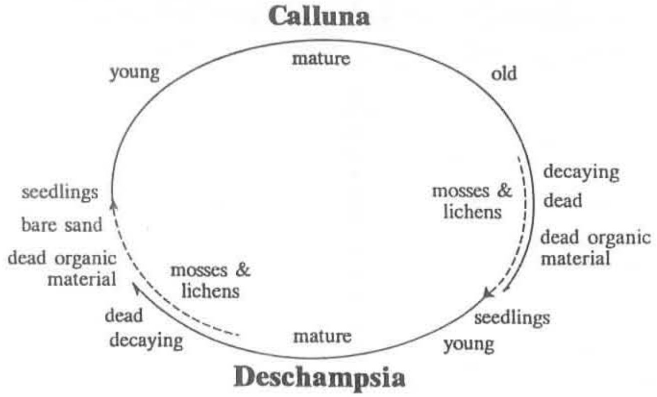

Fig. 2: Scheme of a cyclical vegetation change in heathland.

The shift between *Deschampsia* and *Calluna* leads to the conclusion that the entire system is in transition despite the fact that the nitrogen deposition in the area has not changed considerably. Five subsystems have been distinguished, representing successive stages in the ecosystem development. These subsystems differ not only in species composition and structural features but also in nutrient content and cycling.

I. The continuous shifts in cover, vitality and growth of *Calluna* and *Deschampsia* indicate a cyclic process in this heathland ecosystem development, despite the fact that the nitrogen climate in the area has not changed. The complete sequence of spontaneous development involves two main alternating stages dominated by *Calluna vulgaris* and *Deschampsia flexuosa* respectively. In the transition periods between these, two short transient stages develop, dominated by mosses and lichens, and even bare ground in the transition from dying *Deschampsia* to regenerating *Calluna* (Fig. 2).

II. The existence of this succession sequence provides evidence that heathland ecosystems in the area (at least the ecosystem investigated), reveal their own dynamics which are inherent to and characteristic of these ecosystems, despite the continuous nitrogen deposition.

III. The change of heathland into grassland after regular methods of heathland management have been abandoned forms part of these spontaneous dynamics and cannot be primarily ascribed to anthropogenous influences such as N deposition. Nitrogen input can of course influence the dynamics of these ecosystems (e.g. the length of the *Deschampsia*-dominated stage), but must be seen as a secondary factor.

IV. The development and decay of both *Calluna* and *Deschampsia* in the transition period does not proceed at the same rate over large areas. During this process, the earlier monotonous *Calluna* and *Deschampsia* cover pass through a change in a small-scale mosaic pattern of particular plant species at different 'successional ages', i.e. different stages of spontaneous development. As a result, the diversity of the system will increase in the future.

The question about the driving forces behind the cyclic change in dry heathland ecosystems cannot yet be answered satisfactorily and fully. This research provides evidence of differences in the chemical status of particular subsystems/stages of succession. We hypothesize that changing nutrient status during the succession combined with the physical age of particular species opens a niche for the change in vegetation. Definitive answers to these questions can only be revealed by further research on the functioning of heathland ecosystems.

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